COMPARATIVE LIFE HISTORY AND FLORAL CHARACTERISTICS OF DESERT AND MOUNTAIN FLORAS IN UTAH

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Abstract.— Life forms and floral characteristics of plants at Arches National Park (desert communities), the Mt. Nebo complex, and a subalpine meadow in the Uinta Mountains (montane and subalpine communities) were compared. Characteristics observed were (1) life form, (2) longevity, (3) pollination system, (4) flower structure, (5) flower symmetry, and (6) flower color. Common families in each flora were also compared. Results showed that there is a significant overrepresentation of shrub species at Arches, and an underrepresentation of perennial forbs. Relative number of perennial forb species was significantly higher at Mt. Nebo and the subalpine meadow than at Arches National Park. Native annuals and wind-pollinated species were significantly overrepresented at Arches. Flowers with open structure that permit free access of most insects to nectar and pollen were overrepresented at Mt. Nebo and in the subalpine meadow. The distribution of flower colors also differs significantly among these ecologically contrasting floras, with yellow being best represented in the desert and white in the mountains.

Because of accelerating development of energy and other natural resources, plant communities of the world are constantly being altered. In the United States, law requires that such disturbed areas be restored to their natural condition (Public Law 95-87, 1977), but little is known of the relative proportion of life histories and floral characteristics that enhance coexistence and self-perpetuation of a variety of wild plant species on common sites. What controls the relative success of pollen transfer by wind or animal in various natural communities? Do the contrasting climatic conditions of certain environments affect the success of species of various life forms, longevity, and/or floral characteristics?

In this paper, we compare characteristics of three Utah floras: the floras are from Arches National Park (desert), the Mt. Nebo complex (midelevation montane vegetation), and a subalpine meadow at high elevation in the Uinta Mountains. Arches National Park is a semiarid, cold desert region in southeastern Utah with an average elevation of about 1,220 m above sea level. Its topography consists of rolling hills and sandstone outcrops. The mean annual precipitation at Moab, near Arches, was 21.7 cm with a standard deviation of 4.3 cm (Nat. Oceanic and Atmosph. Admin. 1971–1979). The average annual temperature was 13.5 C. Mt. Nebo and adjacent mountains form a montane habitat with elevations between 1,829 and 3,621 m, but average elevation is in the neighborhood of 2,500 m. Average annual temperatures at Timpanogos Cave (1,720) 73.3 km north of Mt. Nebo was 9.4 C. The mean annual precipitation at Timpanogos Cave was 55.3 cm for the 1971–1979 period and that at the Payson Guard Station (2,454 m) was 73.3 cm with a standard deviation of 11.9 cm (Whaley and Lytton 1978). The Payson Guard Station is 17.4 km north of the crest of Mt. Nebo. The series of subalpine meadows selected for this study are located just below Bald Mountain Pass at the 28-mile marker (45.1 km) on the Mirror Lake Highway (Utah Highway 150) in Summit County, Utah. Average elevation at these meadows is 3,216 m, whereas mean annual precipitation at Trial Lake (near the meadows) was 102.8 cm with a standard deviation of 18.3 cm (Whaley and Lytton 1978). The mean annual temperature of this site is approximately –2.4 C (Callison and Harper, in review).

Jaccard's community coefficient (1912) shows the Arches and Nebo floras to be 90 percent dissimilar, Arches and Bald Mountain 98 percent dissimilar, and the Nebo and Bald

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Mountain floras 90 percent dissimilar. Because these floras are so dissimilar and occupy such physically different ecological situations, it was hypothesized that there would be statistically significant differences in reproductive strategies of the plant species of the three floras. This paper compares the distribution of life form, longevity, and floral characteristics in the three floras. The comparisons evaluate the relative success of various reproductive strategies of plant species native to these three contrasting environments.

Methods

Floristic checklists furnish the data on which this study is based. The list for Mt. Nebo and adjacent mountains, Utah County, was compiled from Collins (1979) and Allred (1975). Checklists for Arches National Park were prepared by Harrison et al. (1964) and Allan (1977). The Bald Mountain meadow checklist was taken from Pendleton (1981).

Life history and floral characteristics were determined for all species from preserved specimens in the Brigham Young University Herbarium. There were 734 species (647 native; 12.0 percent introduced) on the Mt. Nebo complex checklist, 356 (322 native; 9.6 percent introduced) on the desert list (Arches National Park), and 134 (all native) on the high elevation meadow list (Bald Mountain). The following information was obtained for each of the native species: (1) longevity, (2) life form, (3) likely pollinating agent, (4) flower symmetry, (5) flower structure, and (6) flower color. All analyses reported in this paper are based on native species only.

Longevity was simply recorded as annual or perennial. Species described in keys as biennials were treated here as annuals, except those species listed as "biennials to short-lived perennials" were considered perennials. Plant life form was noted as tree, shrub, forb, or grass. In respect to pollination system, plant species were classified as anemophilous or zoophilous. It is realized that some of the species may be self-pollinated, but this could not be determined without independent research on each species. Thus, no attempt was made to identify self-pollinated taxa.

Flower symmetry was regarded as either zygomorphic or actinomorphic. Species were also classified according to flower structure. Structure of zoophilous flowers was described as restricted when access to nectar or pollen was difficult for unspecialized pollinators. Restricted access flowers had long corolla or calyx tubes or had nectaries at the base of long spurs, thus limiting access to pollen or nectar. Flowers classified as open-structured were saucer or bowl shaped and appeared incapable of mechanically excluding any pollinator. Moreover, some plants were considered to be only partially restrictive, having short calyx tubes or deeply lobed and/or widely flaring sympetalous corollas: such flowers were listed as semi-restricted. Flower colors were listed as red, violet, blue, yellow, pink, white, or greenish.

Important families for each location were summarized by the number of species found in each flora. Jaccard's similarity index was employed to test compositional similarity between floras. The Chi-square statistic was used to identify departures from random expectations. In the Chi-square analyses, random expectations are based on the proportion of the species in the pooled floras that share a particular trait (e.g., the proportion of the species in the combined floras from the desert and montane environments that have red flowers). If the trait is randomly distributed between the two floras, the proportion of species having the trait in each flora should not differ significantly from the proportion having that trait in the pooled flora. The Chi-square statistic was used to test whether the observed and expected numbers of species (tests use absolute numbers, not the proportions) sharing a trait in the individual floras differed significantly. If there was a significant departure, the trait was considered to be under- or overrepresented in a given flora. Introduced species were omitted from all analyses on the assumption that they may not have achieved stable reproductive characteristics in their new home.

Results and Discussion

A total of 70 families, 307 genera, and 734 species occurred in the Mt. Nebo flora. There are 60 families, 203 genera, and 356 species reported for the Arches flora. Thirty-six families, 86 genera, and 134 species appear on the Bald Mountain meadows checklist. Jaccard's index (Jaccard 1912) shows the Arches and Nebo floras to be 10.0 percent similar on the basis of species, 32.5 percent similar on the basis of genera, and 75.5 percent similar on the basis of families. The Arches and Bald Mountain floras are 1.5 percent similar on the basis of species, 12.0 percent similar on the basis of genera, and 39.1 percent similar on the basis of families. The Mt. Nebo and Bald Mountain floras show 10.2 percent similarity by species, 23.2 percent by genera, and 45.2 percent by families. Because the families contributing species to these flora are so similar, most of the observed differences in plant adaptations in the three areas can be attributed to ecological selection rather than to differences in basic phylogeny.

Families contributing most of the species in the three floras are reported in Table 1. The families Asteraceae and Poaceae dominate the three floras: Fabaceae holds third place in the Arches flora, Cyperaceae claims that position at Bald Mountain, and Brassicaceae takes that slot on Mt. Nebo. The family Chenopodiaceae contributes over three times as many species in relative terms in the desert as in the mountains. In contrast, species of Rosaceae, Caryophyllaceae, Polemoniaceae, Saxifragaceae, and Scrophulariaceae are twice or more as common in our mountains as in the desert flora considered.

Life Form.— In all three floras, the predominant life form (as represented by number of species) is the broad-leaved herb (forb). At Arches National Park, 64.3 percent of the total flora is contributed by forbs; on Mt. Nebo, 73.0 percent of the species are forbs; and at Bald Mountain, 64.9 percent of the species are forbs (Table 2). Analysis shows that forbs are significantly overrepresented in the midmontane flora, whereas they are underrepresented in the high-elevation meadows and in deserts (Table 3). The shrub life form contributes proportionally over twice as many species in the desert (14.3 percent) as in the mountain floras at Mt. Nebo (7.0 percent) and at Bald Mountain (6.8 percent). That difference is statistically highly significant ($\Sigma X^2 = 30.46$, $P < 0.005$, Table 3A).

The results support the hypothesis that under dry conditions, shrubs are more successful than forbs. Deserts are notorious for unpredictable climatic patterns, and many forbs do not tolerate moisture deficits for long periods (Hironaka 1963, Mueggler 1972, Harner and Harper 1973). Shrubs can tolerate such conditions. They exhibit a variety of adaptations to dry environments, such as deep root systems and reduced reliance on turgor pressure to keep leaves expanded to collect light and carbon dioxide (Sharif and West 1968). Shrubs also have leathery or firm leaves that reduce breakage from heavy winds and are resistant to herbivory; and, finally, shrubs have well-developed secondary meristems

TABLE 1. A comparison of important families showing the number of species and percent (in parenthesis) of the total floras of Arches National Park, the Mt. Nebo complex, and Bald Mountain meadows, Utah.

Family	Arches No. (%)	Mt. Nebo No. (%)	Bald Mtn. No. (%)
Asteraceae	80 (22.5)	115 (15.7)	20 (14.9)
Poaceae	51 (14.3)	105 (14.3)	18 (13.4)
Fabaceae	25 (7.0)	30 (4.1)	2 (1.5)
Chenopodiaceae	22 (6.2)	14 (1.9)	0 (0.0)
Brassicaceae	17 (4.8)	50 (6.8)	4 (3.0)
Scrophulariaceae	10 (2.8)	36 (4.9)	8 (6.0)
Boraginaceae	10 (2.8)	19 (2.5)	1 (0.7)
Cyperaceae	9 (2.5)	16 (2.2)	12 (9.0)
Rosaceae	7 (2.0)	34 (4.6)	4 (3.0)
Liliaceae	7 (2.0)	14 (1.9)	4 (3.0)
Caryophyllaceae	2 (0.6)	18 (2.5)	6 (4.5)
Ranunculaceae	4 (1.1)	28 (3.8)	5 (3.7)
Polemoniaceae	5 (1.4)	19 (2.6)	1 (0.7)
Saxifragaceae	1 (0.3)	18 (2.5)	3 (2.2)
Salicaceae	6 (1.7)	15 (2.0)	1 (0.7)
Other	100 (28.0)	203 (27.7)	45 (33.6)
TOTALS	356 (100.0)	734 (100.0)	134 (100.0)

that probably permit individual roots to be longer lived than is possible for species that lack secondary meristems (as in grasses and sedges). During dry periods, shrubs persist and maintain root systems in both lateral and vertical space; when better moisture conditions do return, herbs attempting to colonize barren spaces between shrubs experience extreme competition from the already established root systems of shrubs. Even in moist years, however, the barren interspaces between shrubs are only sparsely clothed with annual plants, but nearby areas that have been deprived of their shrub cover by abusive grazing or mechanical disturbance support a nearly complete cover of annual plants (Hutchings and Stewart 1953).

Graminoides tend to be better represented in the Arches flora (grasses) and at Bald Mountain (sedges) than at Mt. Nebo. Trees are best represented in the midelevation mountain flora (Table 2).

Longevity.— Longevity of species in the desert and montane floras also show significant differences. The deserts have more annual species than one would expect by chance ($\Sigma X^2 = 21.27$, $P < 0.005$, Table 3B). Native annuals contribute 18.9 percent of the 322 species at Arches National Park, 10.5 percent of the 647 species on the Mt. Nebo

Table 2. Characteristics of the native floras of Arches National Park, the Mt. Nebo complex, and the Bald Mountain meadows. The table shows the number of species and the percent of the native flora (in parentheses).

	Arches No. Sp. (% flora)	Mt. Nebo No. Sp. (% flora)	Bald Mtn. No. Sp. (% flora)
Life form			
Trees	13 (4.0)	39 (6.0)	3 (2.2)
Shrubs	46 (14.3)	45 (7.0)	9 (6.7)
Forbs	207 (64.3)	472 (73.0)	87 (64.9)
Graminoides	56 (17.4)	91 (14.0)	35 (26.1)
Total	322 (100.0)	647 (100.0)	134 (100.0)
Longevity			
Annual	61 (18.9)	68 (10.5)	7 (5.2)
Perennial	261 (81.1)	579 (89.5)	127 (94.8)
Total	322 (100.0)	647 (100.0)	134 (100.0)
Pollination system (annuals excluded)			
Anemophilous	101 (38.7)	162 (28.0)	39 (30.7)
Zoophilous	160 (61.3)	417 (72.0)	88 (69.3)
Total	261 (100.0)	579 (100.0)	127 (100.0)
Flower symmetry (zoophilous species)			
Radial	188 (88.7)	395 (84.4)	77 (83.7)
Bilateral	24 (11.3)	73 (15.6)	15 (16.3)
Total	212 (100.0)	468 (100.0)	92 (100.0)
Flower structure (zoophilous species)			
Open	55 (25.9)	179 (38.2)	42 (45.7)
Restricted	59 (27.8)	128 (27.4)	14 (15.2)
Semirestricted	98 (46.2)	161 (34.4)	36 (39.1)
Total	212 (100.0)	468 (100.0)	92 (100.0)
Flower color (zoophilous species)			
White	50 (23.6)	165 (35.3)	30 (32.6)
Yellow	88 (41.5)	148 (31.6)	23 (25.0)
Blue	20 (9.4)	57 (12.2)	8 (8.7)
Violet	27 (12.7)	36 (7.7)	12 (13.0)
Pink	8 (3.8)	34 (7.2)	12 (13.0)
Red	14 (6.6)	15 (3.2)	1 (1.1)
Green	4 (1.9)	8 (1.7)	5 (5.4)
Other	1 (0.5)	5 (1.1)	1 (1.1)
Total	212 (100.0)	468 (100.0)	92 (100.0)

complex, and only 5.2 percent of the 134 species from the Bald Mountain flora.

Climatic unpredictability enhances the success of annuals in deserts (Schaffer and Gadgil 1975), where precipitation is sporadic and scarce. The annual strategy seems well suited for such conditions, whereas perennial forbs consistently contain high levels of tissue moisture (Sharif and West 1968). Our results show that perennial forbs are underrepresented in the desert (Table 3C).

Pollination Systems.— Because shrubs have been shown to be overrepresented at Arches, and because anemophily is heavily favored among woody species (Ostler and Harper 1978, Freeman et al. 1980), we anticipated that anemophily would be most prevalent at Arches. At Arches National Park, 38.7 percent of the perennial flora is anemophilous; on Mt. Nebo only 28.0 percent and at Bald Mountain only 30.7 percent of the species are wind pollinated (annuals have been omitted from this analysis to minimize the possible confusing effect of self-pollinated species, which are believed to be especially common among annuals [Solbrig 1977]). The differences in modes of pollination in the three floras are statistically significant ($\Sigma X^2 = 9.64$, $P < 0.005$, Table 3D).

The reason that there are more anemophilous species in the desert is not that there is more wind movement there. The Arches area receives only half as much wind (1,590.5 km at Moab) as the Mt. Nebo area (2,984.4

Table 3. Chi-square analyses comparing life histories and floral characteristics of the native plant species of Arches National Park, the Mt. Nebo complex, and the Bald Mountain complex of Utah. Observed and expected numbers of species (in parentheses) are shown. Asterisks indicate significance level: single < .05, double < .010, triple < .005 probability.

	Arches	Mt. Nebo	Bald Mtn.	Summation Chi-square values
Life form				
Trees	13 (16.1)	39 (32.3)	3 (6.7)	
Shrubs	46 (29.2)	45 (58.7)	9 (12.1)	
Forbs	207 (223.6)	472 (449.2)	87 (93.1)	
Grasses	56 (53.1)	91 (106.8)	35 (22.1)	30.46***
Growth cycle				
Annuals	61 (39.7)	68 (79.8)	7 (16.5)	
Perrenials	261 (282.3)	579 (567.2)	127 (117.5)	21.27***
Growth cycle/life form				
Perennial forbs	150 (184.5)	406 (370.7)	76 (76.8)	
Other native species	172 (137.5)	241 (276.3)	58 (57.2)	22.99***
Pollination system (annuals excluded)				
Anemophilous	101 (81.5)	162 (180.8)	39 (39.7)	
Zoophilous	160 (179.5)	417 (398.2)	88 (87.3)	9.64***
Flower structure (for zoophilous species)				
All species considered (annuals included)				
Open	55 (75.8)	179 (167.3)	42 (32.9)	
Restricted	59 (55.2)	128 (121.8)	14 (24.0)	
Semirestricted	98 (81.0)	161 (178.8)	36 (35.2)	19.11***
Only perennial species considered (semirestricted taxa ignored)				
Open	46 (59.2)	160 (156.6)	38 (28.2)	
Restricted	61 (47.8)	123 (126.4)	13 (22.8)	14.35***
Flower color (for zoophilous species)				
Red	14 (8.2)	15 (18.2)	1 (3.6)	
Other	198 (203.8)	453 (449.8)	91 (88.4)	6.70*
White	50 (67.3)	165 (148.5)	30 (29.2)	
Other	162 (144.7)	303 (319.5)	62 (62.8)	9.21**
Yellow	88 (71.1)	148 (157.0)	23 (30.9)	
Other	124 (140.9)	320 (311.0)	69 (61.1)	9.82**

km at Lehi) in the April–September period (Whaley and Lytton 1979). Conditions that may favor wind-pollinated species at Arches include dominance of most perennial covers by a few woody species that have large populations, low-growing, open vegetation, and severe, unpredictable periods of drought. Accurate wind movement readings were not available for the Bald Mountain area.

When only perennial species are considered, woody species are much better represented in the Arches flora (22.6 percent) than at Mt. Nebo (14.5 percent) or Bald Mountain (9.4 percent). Furthermore, shrubs dominate all major communities at Arches (Allan 1977). Diversity of perennial species as measured by number of species per 1.0 m^2 (a variable known to reduce the success of wind-pollinated taxa [Ostler et al. 1982]) is shown by Allan (1977) to be 2.6 at Arches (10 communities considered) as compared with 4.3 in the Wasatch Mountains (of which Mt. Nebo is a part [Ostler and Harper 1978, 25 communities reported]) and 6.9 at Bald Mountain (Pendleton 1981, 4 communities reported). Wind pollination is further facilitated at Arches by a plant cover that is more open than that at Nebo. Allan (1977) reported an average of 41.3 percent living cover at Arches, but, considering the fact that 70 percent of the Mt. Nebo study area is dominated by oak woodland or forests of aspen and/or conifer, plant cover there undoubtedly averages well over 65 percent (see Allan 1962, Crowther and Harper 1965, Kleiner 1966, and Harper 1981 for cover estimates for similar vegetations in northern Utah). Vegetative cover in subalpine meadow in the Uinta Mountains averages about 76 percent (Ostler et al. 1982). Finally, annual precipitation is more likely to fall below a level sufficient to support flowering of many species at Arches than in the mountain study areas. Frequent years of sparse or no flowering distributed at random through time should reduce the likelihood that insect pollinators can maintain large enough populations to pollinate all the flowers produced in years of adequate soil moisture. Wind-pollinated species should be favored in such situations provided individual plants are large enough to intercept a reliable flow of air, foliage cover is not so dense that it seriously interferes with pollen movement in the wind, and conspecific individuals are close enough together to insure that most stigmas will receive pollen. On all counts, the Arches area is better suited for wind pollination than the two mountain locations.

Flower Structure.— If reproduction of animal-pollinated species is to be successful, floral structure should encourage the likelihood of sequential visits by specific pollinators. When flowers of coexisting species compete for pollinators, species having flowers that mechanically exclude many kinds of pollinators should be able to conserve more nectar or pollen for adapted visitors than species whose flowers can be worked by any visitor. Thus visits by such adapted pollinators should be reinforced by more dependable nectar or pollen rewards, thus encouraging the pollinator to seek out other flowers of the same type. As a result, flowers with restricted access should be at a reproductive advantage in diverse assemblages of plants that flower simultaneously.

Ostler and Harper (1978) show that flowers that have restricted access to the nectar and/or pollen supply are positively correlated with the diversity of animal-pollinated species per unit area in the Wasatch Mountains of Utah and Idaho. Thus, one might be tempted to hypothesize that, because diversity is lower at Arches than in Utah mountains as noted above, one could expect an overrepresentation of open-structured flowers in the desert. The data show, however, that when all species are considered, the mountain floras have relatively more species with open flowers than the desert ($\Sigma X^2 = 19.11$, $P < 0.005$, Table 3E). Even among perennial species only, that pattern continues to hold ($\Sigma X^2 = 14.35$, $P < 0.005$, Table 3E).

The difference in flower structure among the floras of Arches, Bald Mountain, and Mt. Nebo may be attributable to differences in flowering phenology. Species must flower when moisture conditions are favorable. In the desert, moisture conditions for most species are apparently optimal in the spring, because it is at that time that most desert species flower. Accordingly, although there are fewer species per unit area in the desert, more species may actually flower simultaneously than in the mountain zone. Thus, at certain times, there may be greater competition among plant species for pollinating animals in the desert than in at least midelevation mountains.

In contrast to deserts, midelevation mountain communities have favorable moisture conditions throughout much of the growing season. It is therefore possible for coexisting species to partition the available time by flowering out of synchrony. Such out-of-phase flowering should decrease competition for pollinators and allow for more open flowers (Mosquin 1971). This argument probably does not hold at high elevations where growing seasons are short and flowering of all species is confined to that brief season. In such environments, simultaneous flowering of many species is undoubtedly commonplace. The profusion of open-flowered taxa in the subalpine meadows (Table 2) thus cannot be attributed to low flowering-plant diversity.

It has become clear in recent years that pollinating insect faunas are larger and more diverse in warmer and lower elevation environments than in cold and/or high elevation habitats (Arroyo et al. 1982, Warren et al. 1982). Hymenopteran insects especially appear to decline in colder and higher elevation communities, and Dipteran and Lepidopteran pollinators become relatively more important. It has long been recognized that Hymenopteran pollinators are the most efficient of all insects at manipulation of complex flowers (Faegri and Pijl 1971). It is thus possible that the observed predominance of open flowers in our mountain floras is related to changes in composition of the pollinator fauna along the altitudinal gradient. Open flowers may be favored when there is competition among flowers for an impoverished and less efficient guild of pollinating insects.

Flower Symmetry.— The native flora of Arches National Park consists of 88.7 percent radially symmetrical and 11.3 percent zygomorphic-flowered species. The Mt. Nebo flora includes 84.4 percent radial and 15.6 percent zygomorphic flowers. Finally, the Bald Mountain Flora consists of 83.7 percent radial and 16.3 percent zygomorphic flower (Table 2). Although differences between the three floras are not statistically significant ($\Sigma X^2 = 2.42$), there is a trend toward a greater number of zygomorphic flowers as elevation and diversity increases. Zygomorphic structure is believed to force insects to approach flowers in more stereotyped ways. Thus, in zygomorphic flowered taxa, mutations that result in loss of stamens and stigmas off the regular access route of the insect to the floral reward (nectar and/or pollen) could be accommodated without loss in fecundity. In harsh environments where carbohydrate gains are marginal, zygomorphy and the energy economy associated with reduced numbers of reproductive parts and lower pollen production could be expected to have selective advantages.

Flower Color.— Is there any difference in the distribution of colors among these floras? Ostler and Harper (1978) showed that floral color diversity was positively correlated with species diversity of the communities studied. Our data demonstrate that red and yellow flowers are overrepresented at Arches National Park (Table 3F), with the differences being statistically significant for both ($P < 0.05$ or better). White flowers are significantly overrepresented at Mt. Nebo and Bald Mountain. White seems to be favored in moist and wooded environments (Ostler and Harper 1978, Del Moral and Standley 1979), whereas yellow flowers are consistently better represented in dry environments (Kevan 1972, Tikhomirov 1966, and Weevers 1951). The results for white flowers were expected in the Nebo flora (but not at Bald Mountain meadow), because white color had been shown to be more abundant in forest understories by both Ostler and Harper (1978) and Del Moral and Stanley (1979). The Mt. Nebo complex is largely dominated by forest or woodland communities, but there is only a minor amount of woodland at Arches National Park and Bald Mountain. Ostler and Harper (1978) speculated that white flowers reflected more light and were more easily found by pollinators in forest understories. Baker and Hurd (1968) noted that moths tend to replace bees as major pollinators in shaded habitats, and moths show a preference for white flowers. Finally, it is possible that the insect eye, like that of the human, is unable to perceive color at low light intensities (Proctor and Proctor 1978). Thus, the insect may react to flower color in shaded environments in terms of contrast alone rather than in terms of different hues per se.

The abundance of white flowers in the subalpine meadows cannot be explained by the foregoing argument. At this point, we can only hypothesize that the importance of white flowers and the diminished abundance of yellow-flowered species in high elevation meadows is somehow related to the cooler, more moist environment or to altered composition of the pollinating insect community (or both) at high elevations.

The proportionally greater number of red and, to a lesser extent, yellow flowers in the Arches flora seems attributable to the nearness of the park to areas of high diversity of hummingbird species in Arizona (up to nine species, see Crosswhite and Crosswhite 1981). Hummingbirds are believed to have been the selective force responsible for the evolution of many orange- and red-flowered species in the American Southwest (Crosswhite and Crosswhite 1981). At the mountain sites, such "hot"-colored species are relatively less common (Table 2). Only four species of hummingbirds occur in the Mt. Nebo area, and three hummingbird species occur infrequently at the high subalpine meadows considered here.

Conclusion

The results demonstrate that there are definite differences in the distribution of plant longevity, life form, mode of pollination, floral structure, and flower colors in the desert and mountain floras compared in this study. Annuals and shrubs are overrepresented in the Arches National Park flora, and zoophily is significantly more abundant in the mountain floras. Open-structured flowers are significantly overrepresented on the mountain floras. White flowers are most common in the mountain floras, whereas red and yellow flowers are best represented in the desert.

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